

Osmotically driven flows and maximal transport rates in systems of long, linear porous pipes.

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We study the flow of water and solutes in linear cylindrical pipes with semipermeable walls (membranes), driven by concentration differences across the membranes, inspired by the sieve tubes in conifer needles. The aim is to determine the efficiency of such systems. For single pipes, we assume that the velocity at the entrance (the tip of the needle) is zero, and we determine the velocity profile throughout the pipe and the outflow at the end of the pipe, where the pressure is specified. This is done for the particular case where the concentration of the solute is constant inside the pipe, and it is shown that the system has a characteristic length scale $L_{\text{eff}} \sim r_0^{3/2} (L_p \eta)^{-1/2}$, where r_0 is the pipe radius, L_p is the permeability of the wall and η is the viscosity of the fluid. Osmotic flows in pipes with lengths $L \gg L_{\text{eff}}$ will contain a stagnant zone from the entrance, where the velocity is very small. The outflow comes from a region of length L_{eff} near the end, and the increase of velocity, if the pipe is made longer, is marginal. We show that relaxing the assumption of constant solute concentration c_0 cannot lead to larger outflows, as long as the local concentration never exceeds c_0 . We determine the viscous dissipation for a single pipe and the result for the total dissipation, including bulk dissipation in the pipe and the flow through the pores of the membrane (modelled as a systems of cylindrical pipes), is $\dot{W}_{\text{tot}} = - \int_0^L RT c'(x) Q(x) dx + (RT c(L) - p(L)) Q(L) - (RT c(0) - p(0)) Q(0)$ where $Q(x)$ is the flow rate, $p(x)$ is the pressure and L is the length of the pipe. We finally generalise these results to systems of interacting parallel, cylindrical pipes with a power law distribution of lengths (as in the sieve tubes of conifer needles). For constant concentration we give an analytical solution for the velocity profile in terms of modified Bessel functions and show that the results are surprisingly similar to the single pipe results regarding the stagnant zone and value of L_{eff} . The biological context and some of the mathematical results have been described in [1].

I. INTRODUCTION

In this paper we present analytical results for stationary flows in systems of straight pipes with porous, semipermeable walls, driven by osmotic water uptake. Such systems are found in the sieve tubes of the phloem in plant leaves, which are responsible for the sugar export (see e.g., [2]), and our results pertain in particular to leaves with a linear vein-architecture, such as conifer needles and grass leaves. A central aim is to determine the maximal flow rates, and thus solute transport rates, such systems can carry. The biological context has been described in [1], where also many of the results for single tubes have been given. For definiteness, we shall call the solute “sugar”, although it could be basically anything soluble, which cannot pass the pipe walls.

We shall first discuss the flow in a single tube, closed in one end (or with the velocity specified), representing the interior of the leaf or needle, and open in the other end, representing the outlet to the petiole, where we specify pressure or resistance. Sugar is assumed to be loaded into the tube by some mechanism (see e.g., [2]), and we study in particular the case where this loading mechanism is able to keep the sugar concentration constant throughout the pipe, since we shall show that this is the configuration carrying the largest flow. We shall derive both flow rates and energy dissipation, including also the dissipation of the flow through the membrane wall.

We shall continue with flows in systems of coupled linear pipes, using the methods developed in [3], and present analytical solutions for flow rates and dissipation, again in the constant concentration case.

II. THE MÜNCH-HORWITZ EQUATIONS FOR A SINGLE PIPE

We consider a system as shown in Fig. 1 with an open permeable pipe or tube inside a medium. In plants the sieve tubes of the phloem are roughly of this form, and in the leaves their radii (r_0) are in the μm regime while their length (L) is centimetric. The slender (lubrication) approximation used by [4] to describe such flows is thus extremely well-suited. He showed that in the lubrication approximation, the stationary flow field has the form

$$v_r(r, x) = f(r)v_0(x) \quad (1)$$

$$v_x(r, x) = g(r)V_0(x) \quad (2)$$

where

$$f(r) = \frac{r^3}{r_0^3} - 2\frac{r}{r_0} \quad (3)$$

$$g(r) = \left[1 - \frac{r^2}{r_0^2}\right] \frac{4}{r_0} \quad (4)$$

and where $v_0(x)$ is the radial osmotic inflow given by

$$v_0(r, x) = v_r(r_0, r) = L_p [RTc(r_0, x) - p(r_0, x)] \quad (5)$$

and

$$V_0(r, x) = \left[1 - \frac{r^2}{r_0^2}\right] \frac{4}{r_0} \int_0^x v_0(x') dx'. \quad (6)$$

In the lubrication approximation the pressure does not vary over the pipe cross-section. If the solute is also “well-stirred”, we can drop the r -dependence also for the concentration and replace the boundary condition (6) by a mean value expressed in terms of the average fields $u(x) = \bar{v}_x(r, x) = (2/r_0)V_0(x)$, $c(x) = \bar{c}(r, x)$ and $p(x) = \bar{p}(r, x)$, averaged over the cross-section. This can be done if the radial Péclet number $\text{Pe} = v_0 L/D$, where D is the molecular diffusion, is small enough (see Jensen *et al.* [2] for more details), and one finds for the average fields:

$$\frac{du}{dx} = \frac{2L_p}{r_0} (RTc(x) - p(x)) \quad (7)$$

and similarly for the flow rate $Q(x)$

$$\frac{dQ}{dx} = \pi r_0^2 \frac{du}{dx} = 2\pi r_0 L_p (RTc(x) - p(x)). \quad (8)$$

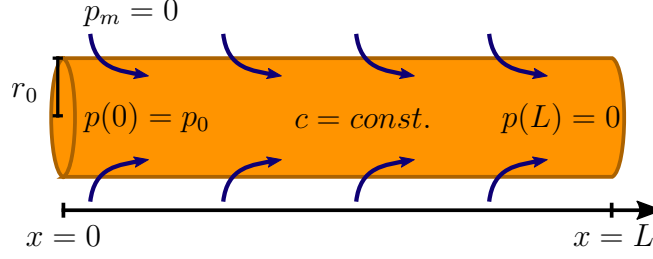


FIG. 1. A single tube of length L and circular cross-section of radius r_0 , closed on one side, is filled with solute of constant concentration c . Water is osmotically dragged in from the surrounding medium and creates a bulk flow along the tube in positive x -direction.

The pressure varies along the tube following Darcy's law:

$$\frac{dp}{dx} = -\frac{8\eta}{r_0^2}u(x). \quad (9)$$

These equations (called the Münch-Horwitz equations) should be supplemented by an equation for the sugar loading, the reaction-diffusion equation

$$\frac{d(uc)}{dx} = D\frac{d^2c}{dx^2} + \Upsilon(x), \quad (10)$$

defining the loading function $\Upsilon(x)$. In the following, we shall assume that this loading function is able to keep the concentration $c(x)$ constant $= c$ throughout the tube. This does not seem far from the situation in many plants and it is close to the situation obtained from “target concentration” models [5]. We shall later show that this situation is actually optimal, in the sense that no concentration profile, limited everywhere by the value c , can generate larger flows than the constant one where $c(x) = c$ everywhere. Thus dropping the x -dependence on c , we can differentiate (7) and insert (9) to obtain

$$\frac{d^2u}{dx^2} = -\frac{2L_p}{r_0}\frac{dp}{dx} = \frac{16\eta L_p}{r_0^3}u(x) \quad (11)$$

With the Münch number

$$M = \frac{16\eta L_p L^2}{r_0^3}, \quad (12)$$

using the characteristic velocity and pressure scales as

$$u^* = \frac{2LL_p RTc}{r_0} \quad (13)$$

$$p^* = RTc \quad (14)$$

and thus dimensionless variables

$$s = x/L \quad (15)$$

$$U(x) = u/u^* \quad (16)$$

$$P(x) = p/p^* \quad (17)$$

we can rewrite the equations as

$$\frac{dU}{ds} = c(s) - P(s) \quad (18)$$

$$\frac{dP}{ds} = -M U(s) \quad (19)$$

showing that the Münch number M is actually the only coefficient left. The square root of the Münch number will recur frequently, so we shall give it its own symbol m . If we introduce the “wall length”

$$l_0 = \eta L_p \quad (20)$$

which is a material parameter describing the porosity of the pipe (actually more the ratio of the area of the pores in the porous wall to their length, see later) and typically has values around 10^{-17} m in plants, we can write m in terms of two important aspect ratios

$$\alpha = \frac{r_0}{L} \quad (21)$$

which is the aspect ratio of the system, typically around 10^{-3} in conifer leaf veins, and

$$\beta = \frac{l_0}{r_0} \quad (22)$$

with typical values around 10^{-11} . Then

$$m = \sqrt{M} = 4 \frac{\sqrt{\beta}}{\alpha} \quad (23)$$

which is *independent* of L . When L (or m) becomes large, the velocity scale u^* defined in (13) becomes much larger than the typical velocities. As we shall see in the following, we would get a better value for the characteristic velocity by replacing L in (13) by the value

$$L_{\text{eff}} = \frac{L}{m} = \frac{r_0^{3/2}}{(16L_p\eta)^{1/2}}, \quad (24)$$

A. Solution with constant concentration

We now solve (11) in the form

$$\frac{d^2 U}{ds^2} = m^2 U(s). \quad (25)$$

with the general solution

$$U(s) = A \sinh(ms) + B \cosh(ms) \quad (26)$$

with the constants A and B to be determined. As a boundary condition, we assume that the velocity at the beginning of the tube is known

$$u(0) = U_0 \quad (27)$$

which determines

$$B = U_0. \quad (28)$$

Together (7) and the first derivative of (26) give A in terms of the pressure at the beginning of the tube $P(0) = P_0$, as:

$$A = m^{-1} (1 - P_0) \quad (29)$$

To determine P_0 , we integrate (19):

$$P(L) = P_0 - m^2 \int_0^1 U(s) ds = P_0 + (1 - P_0) (1 - \cosh m) - m U_0 \sinh m \quad (30)$$

or

$$1 - P_0 = \frac{1 - P(1)}{\cosh m} - m U_0 \tanh m \quad (31)$$

Using this result in (29) we get the final expression for U :

$$U(s) = \frac{1}{m} (1 - P(L)) \frac{\sinh(ms)}{\cosh m} + \frac{U_0}{\cosh m} (\cosh m \cosh(ms) - \sinh m \sinh(ms)) \quad (32)$$

$$= \frac{1}{m} (1 - P(L)) \frac{\sinh(ms)}{\cosh m} + \frac{U_0}{\cosh m} \cosh(m(1-s)) \quad (33)$$

The velocity reached at the end of the tube is then

$$U(1) = \frac{1}{m} (1 - P(L)) \tanh m + \frac{U_0}{\cosh m}. \quad (34)$$

For the special case

$$U_0 = 0 \quad (35)$$

$$P(L) = 0 \quad (36)$$

we get the simple results

$$U(s) = \frac{1}{m} (1 - P(L)) \frac{\sinh(ms)}{\cosh m} \quad (37)$$

$$U(1) = \frac{1}{m} (1 - P(L)) \tanh m \quad (38)$$

$$1 - P_0 = \frac{1 - P(1)}{\cosh m} \quad (39)$$

Returning to dimensional variables, the solutions (for $u_0 = 0$) are

$$u(x) = \frac{2L_p L}{r_0 m} (RTc - p(L)) \frac{\sinh\left(m \frac{x}{L}\right)}{\cosh m} \quad (40)$$

$$Q(x) = \frac{2\pi r_0 L_p L}{m} (RTc - p(L)) \frac{\sinh\left(m \frac{x}{L}\right)}{\cosh m} \quad (41)$$

$$RTc - p_0 = \frac{RTc - p(L)}{\cosh m} \quad (42)$$

B. The stagnant zone

As one can see in Fig. 2, the velocity field (37) has a scale set by $m = \sqrt{M}$, corresponding to a length

$$L_{\text{eff}} = \frac{L}{m} = \frac{r_0^{3/2}}{(16L_p \eta)^{1/2}}, \quad (43)$$

independent of L . Pipes that are substantially larger than this length will carry very little additional current, and the reason is that the velocity remains very small until a distance of approximately L_{eff} from the tip. To make this more clear we can rewrite (40) as

$$u(s) = u_{\text{max}} \frac{\sinh\left(\frac{L}{L_{\text{eff}}} s\right)}{\cosh \frac{L}{L_{\text{eff}}}} \quad (44)$$

with

$$u_{\text{max}} = \frac{2L_p L_{\text{eff}}}{r_0} (RTc - p(L)) \quad (45)$$

If we fix u_{max} , u will vary along the tube as shown in Fig. 2, for different L . Note that the slope of the curves at small s (i.e., $m \cosh^{-1} m$) is a non-monotonic function of m with a maximum at $m = L/L_{\text{eff}} \approx 1.2$. Fig. 3 shows the velocity at the end of the pipe

$$u(1) = u_{\text{max}} \tanh \frac{L}{L_{\text{eff}}} \quad (46)$$

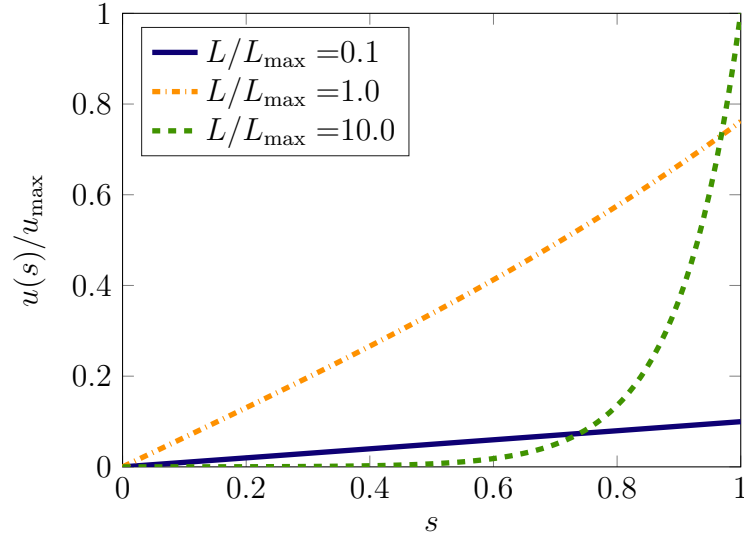


FIG. 2. Velocity along a single pipe for different L/L_{eff} as given by Eq. 44, normalized by u_{max} given by (45).

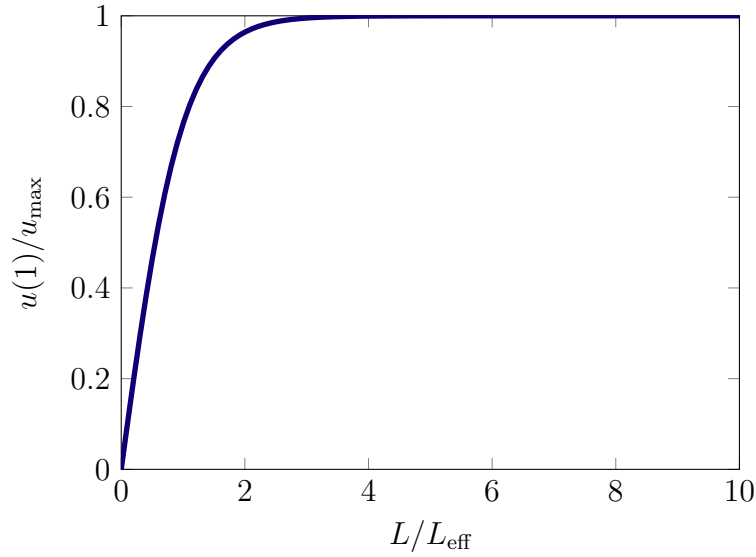


FIG. 3. Velocity at the end of a single tube as given by Eq. 46, normalized by u_{max} given by (45).

which approaches u_{max} for large L/L_{eff} . In that regime, very little is gained by making the pipe longer: the sugar is only transported within the last segment of length of the order L_{eff} , and the output flux remains fixed at u_{max} . Thus the entire region from the tip to a distance L_{eff} from the base will be basically stagnant. It is interesting that the expression for the effective length is independent of the concentration c . In fact one can take $c = 0$ and drive the fluid through the porous walls by making the pressure inside the tube smaller than the external one. This is what happens in the xylem tubes in the root hairs, which contain water with (essentially) no solutes, driven by the tension created by the leaves. This suction-driven flow was analysed in [6], and the characteristic length (43) was identified as the length of the part of the root hair which is responsible for essentially all the water uptake.

III. SOLUTION FOR NON-CONSTANT CONCENTRATION

For non-constant concentration $c(x)$ it is advantageous to rewrite the Münch-Horwitz equations slightly. Differentiating (19) and inserting into (18) gives

$$\frac{d^2 P}{ds^2} - m^2 P = -m^2 C(s) \quad (47)$$

where P and C have been scaled with the maximal concentration c_0 in the pipe: $C(s) = c(x)/c_0$ and $P(s) = p(x)/(RTc_0)$ and we want to solve the boundary value problem

$$P'(0) = -m^2 U(0) = 0 \quad (48)$$

$$P(1) = P_1 \quad (49)$$

For constant concentration $c(s) = c_0$ we get the solution

$$c_0 - P(s) = \frac{c_0 - P_1}{\cosh m} \cosh(ms) \quad (50)$$

and

$$U(s) = -\frac{1}{m^2} P'(s) = \frac{c_0 - P_1}{m \cosh m} \sinh(ms) \quad (51)$$

corresponding to Eq. (38) above. Using the variable $y(s) = c_0 - P(s)$, we (47) becomes

$$\frac{d^2 y}{ds^2} - m^2 y = m^2 (c(s) - c_0) \quad (52)$$

where the boundary conditions now are:

$$y'(0) = -p'(0) = m^2 u(0) = 0 \quad (53)$$

$$y(1) = c_0 - p_1 = y_1. \quad (54)$$

We divide this into a inhomogeneous differential equation with homogeneous boundary conditions

$$\frac{d^2 y}{ds^2} - m^2 y = f(s) \quad (55)$$

with

$$y'(0) = y(1) = 0 \quad (56)$$

and a homogeneous differential equation with inhomogeneous boundary conditions:

$$\frac{d^2 y}{ds^2} - m^2 y = 0 \quad (57)$$

with

$$y'(0) = 0 \quad (58)$$

and

$$y(1) = y_1. \quad (59)$$

The latter *homogeneous* equation has the solution

$$\frac{d^2 y_h}{ds^2} - m^2 y_h = 0 \quad (60)$$

with the *inhomogeneous* boundary conditions

$$y'_h(0) = 0 \quad (61)$$

and

$$y_h(1) = y_1. \quad (62)$$

Choosing

$$y_h(s) = A \sinh ms + B \cosh ms \quad (63)$$

we get $y'_h(0) = Av \cosh vs = 0$ implying that $A = 0$. Further $y_h(1) = B \cosh v = y_1$ implies that

$$B = \frac{y_1}{\cosh m} \quad (64)$$

so

$$y_h(s) = \frac{y_1}{\cosh m} \cosh ms. \quad (65)$$

A. Green's function for the inhomogenous problem

The Green's function satisfies

$$\frac{d^2 G(s, \xi)}{ds^2} - m^2 G(s, \xi) = \delta(s - \xi) \quad (66)$$

or, denoting derivatives by subscripts,

$$G_{ss}(s, \xi) - m^2 G(s, \xi) = 0 \quad \text{for } s \neq \xi \quad (67)$$

with

$$G_s(0, \xi) = 0 \quad (68)$$

$$G(1, \xi) = 0 \quad (69)$$

$$G(s = \xi^+, \xi) = G(s = \xi^-, \xi) \quad (70)$$

(continuity of G at $s = \xi$)

$$G_s(s = \xi^+, \xi) = G_s(s = \xi^-, \xi) + 1 \quad (71)$$

(discontinuity of G_s at $s = \xi$). The general solution of (67) is

$$G(s, \xi) = A_1(\xi) \sinh ms + B_1(\xi) \cosh ms \quad \text{for } s < \xi \quad (72)$$

$$G(s, \xi) = A_2(\xi) \sinh ms + B_2(\xi) \cosh ms \quad \text{for } s > \xi \quad (73)$$

and applying the additional conditions at the boundary and in the interior ($s = \xi$) we get

$$G(s, \xi) = G_<(s, \xi) = \frac{\sinh m\xi \cosh ms}{m} - \frac{\cosh m\xi \cosh ms}{v} \tanh m \quad \text{for } s < \xi \quad (74)$$

$$G(s, \xi) = G_>(s, \xi) = \frac{\cosh m\xi \sinh ms}{m} - \frac{\cosh m\xi \cosh ms}{v} \tanh m \quad \text{for } s > \xi. \quad (75)$$

B. The complete solution

The complete solution can now be written in terms of the inhomogeneity: $f(s)$ as

$$\begin{aligned}
y(s) &= y_h(s) + \int_0^1 G(s, \xi) f(\xi) d\xi \\
&= y_h(s) + \int_0^s G_>(s, \xi) f(\xi) d\xi + \int_s^1 G_<(s, \xi) f(\xi) d\xi \\
&= \frac{y_1}{\cosh m} \cosh ms + \int_0^s \left(\frac{\cosh m\xi \sinh ms}{m} - \frac{\cosh m\xi \cosh ms}{m} \tanh m \right) f(\xi) d\xi \\
&\quad + \int_s^1 \left(\frac{\sinh m\xi \cosh ms}{m} - \frac{\cosh m\xi \cosh ms}{m} \tanh m \right) f(\xi) d\xi \\
&= \frac{y_1}{\cosh m} \cosh ms - \frac{\tanh m \cosh ms}{m} \int_0^1 \cosh m\xi f(\xi) d\xi + \frac{\sinh ms}{m} \int_0^s \cosh m\xi f(\xi) d\xi \\
&\quad + \frac{\cosh ms}{m} \int_s^1 \sinh m\xi f(\xi) d\xi
\end{aligned} \tag{76}$$

Returning to the original variables $f(s) = m^2(c(s) - c_0)$, $P(s) = c_0 - y(s)$ and

$$U(s) = -\frac{1}{m^2} P'(s) = \frac{1}{m^2} y'(s) = \frac{1}{m^2} y'(s) \tag{77}$$

we find

$$\begin{aligned}
U(s) &= \frac{c_0 - P_1}{m \cosh m} \sinh ms - \frac{\tanh m \sinh ms}{v^2} \int_0^1 \cosh m\xi f(\xi) d\xi \\
&\quad + \frac{\cosh ms}{m^2} \int_0^s \cosh v\xi f(\xi) d\xi + \frac{\sinh ms}{m^2} \int_s^1 \sinh m\xi f(\xi) d\xi
\end{aligned} \tag{78}$$

or

$$\begin{aligned}
U(s) &= \frac{c_0 - p_1}{v \cosh v} \sinh vs - \tanh v \sinh vs \int_0^1 \cosh m\xi (c(\xi) - c_0) d\xi \\
&\quad + \cosh vs \int_0^s \cosh v\xi (c(\xi) - c_0) d\xi + \sinh ms \int_s^1 \sinh m\xi (c(\xi) - c_0) d\xi.
\end{aligned} \tag{79}$$

For the output, we get

$$\begin{aligned}
U(1) &= \frac{c_0 - P_1}{m} \tanh m - \frac{\sinh^2 m}{\cosh m} \int_0^1 \cosh m\xi (c(\xi) - c_0) d\xi \\
&\quad + \cosh m \int_0^1 \cosh m\xi (c(\xi) - c_0) d\xi \\
&= \frac{c_0 - P_1}{m} \tanh m + \frac{1}{\cosh m} \int_0^1 \cosh m\xi (c(\xi) - c_0) d\xi
\end{aligned} \tag{80}$$

and the sugar-output is $Q(1) = U(1)c(1)$. In other words

$$U(1) = U_0(1) + \frac{1}{\cosh m} \int_0^1 \cosh m\xi (c(\xi) - c_0) d\xi \tag{81}$$

where $U_0(1)$ is the output flow velocity (51) for constant concentration $c = c_0$. If $c(s)$ never exceeds c_0 , the integral in (81) cannot be positive, and the maximal velocity achievable is therefore the one found for the constant concentration case.

IV. VISCOUS DISSIPATION

We shall determine the viscous dissipation in the flows studied in Sec. 2, by looking firstly at the dissipation in the bulk flow, and secondly at the flow through the porous semipermeable walls.

A. Dissipation in the bulk flow

The viscous dissipation for an axially symmetric flow, such as the Aldis flow field given by Eq. (1)-(2), can be written as

$$\dot{W} = 2\eta \int dV \left[\left(\frac{\partial v_r}{\partial r} \right)^2 + \left(\frac{v_r}{r} \right)^2 + \left(\frac{\partial v_x}{\partial x} \right)^2 + \frac{1}{2} \left(\frac{\partial v_r}{\partial x} + \frac{\partial v_x}{\partial r} \right)^2 \right]. \quad (82)$$

For the Aldis flow we can further write the velocity components in the separated form

$$v_r = f(r)v_0(x) \quad (83)$$

$$v_x = g(r)V_0(x) \quad (84)$$

with

$$V_0'(x) = v_0(x) \quad (85)$$

and the flow rate is

$$Q(x) = 2\pi r_0 V_0(x). \quad (86)$$

To obtain the Aldis solution, we made the assumption that $v_r \ll v_x$ and $\partial/\partial x \ll \partial/\partial r$, so the dominant term in the dissipation is

$$\dot{W}_{\text{lub}} = \eta \int dV \left(\frac{\partial v_x}{\partial r} \right)^2 = \eta \int dV (g'(r))^2 V_0^2(x) = \frac{8\eta}{r_0^4} \int_0^L Q^2(x) dx \quad (87)$$

where we have used that $g'(r) = -8r/r_0^3$. Using the Darcy relation (9) this can be written

$$\dot{W}_{\text{lub}} = - \int_0^L p'(x) Q(x) dx \quad (88)$$

and for a normal Poiseuille flow in a cylindrical pipe with solid walls this becomes $Q\delta p$ as it should. The additional terms in (82) can be written in ascending orders of $1/r_0^2$ as

$$\begin{aligned} \Delta \dot{W}_{\text{add}} &= \frac{11}{48\pi} \int_0^L (Q'')^2 dx \\ &+ \frac{1}{3\pi} \frac{\eta}{r_0^2} \left(5 \int_0^L (Q')^2 dx + 8 (Q'(L)Q(L) - Q'(0)Q(0)) \right). \end{aligned} \quad (89)$$

and in order of magnitude they correspond to replacing 2 or 4 factors of r_0 by factors of L and it would thus not be justified to keep them in the lubrication limit used to obtain Eq. (1)-(2).

B. Dissipation of the flow through the pores of the wall

We make the assumption that the surface of the tube is a semipermeable membrane with N same-sized, cylindrical pores of radius a and length d , where d is the thickness of the membrane (see Fig. 4). We expect this model to be useful, even though, in the context of plant leaves the pores (aquaporins) are of nanometric size, which implies that neither the approximation of cylindrical pores nor the validity of the Navier-Stokes equation is well-founded. The density n of pores, per length, is assumed constant, so $n = N/L$. Through each of the pores we assume a Poiseuille flow with resistance

$$R_i = \frac{\Delta \Pi_i}{q_i} = \frac{8\eta d}{a^4}. \quad (90)$$

The total resistance R of all pores in parallel is related to the permeability L_p :

$$\frac{1}{R} = \frac{N}{R_i} = \frac{N(L)a^4}{8\eta d} \equiv 2\pi r_0 L L_p \quad (91)$$

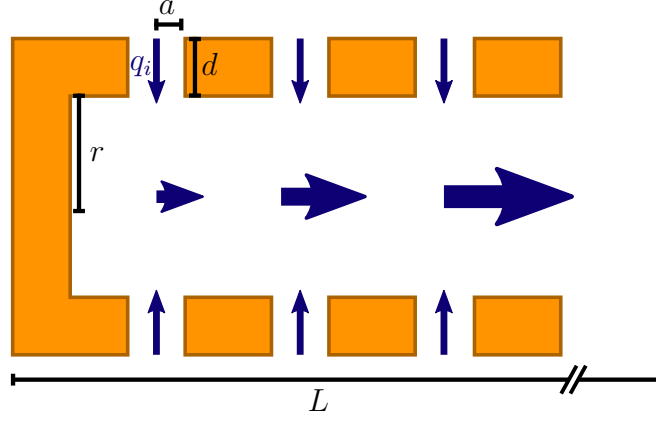


FIG. 4. A membrane tube with pores of radius a and length d .

giving the relation

$$L_p = \frac{na^4}{16\pi\eta d}. \quad (92)$$

The dissipation inside the pore is dependent on the choice of pore radius a and covering fraction ϕ , since this determines the actual inflow velocity $v_i(x)$. With the covering fraction

$$\phi = \frac{n\pi a^2}{2\pi r_0}, \quad (93)$$

they are connected as

$$v_0(x)2\pi r_0 dx = v_i(x)n\pi a^2 dx \quad (94)$$

or

$$v_0(x) = \phi v_i(x). \quad (95)$$

The viscous dissipation through all pores in the membrane is

$$\begin{aligned} \dot{W}_{\text{mem}} &= \frac{8\eta d}{a^4} n \int_0^L q_i^2(x) dx \\ &= \frac{8\eta d}{a^4} n\pi^2 a^4 \int_0^L v_i^2(x) dx \\ &= \frac{8\eta d}{a^4} \frac{n\pi^2 a^4}{\phi^2} \int_0^L v_0^2(x) dx \\ &= \frac{2\pi r_0}{L_p} \int_0^L v_0^2(x) dx \end{aligned} \quad (96)$$

$$= \frac{1}{2\pi r_0 L_p} \int_0^L (Q'(x))^2 dx \quad (97)$$

We might wonder, whether it is valid to retain this term compared to the terms in Eq. (89), which we discarded. In particular, the last term in (89) part of which has precisely the same form as (97). The ratio of the coefficients is roughly $(\eta/r_0^2)r_0 L_p = \eta L_p/r_0 = l_0/r_0 = \beta$, which was indeed assumed to be small. Using the governing equation (7), we can rewrite (97) as

$$\dot{W}_{\text{mem}} = \int_0^L (RTc(x) - p(x))Q'(x) dx \quad (98)$$

and it can thereby be combined elegantly with the resistance in the pipe (88). The total dissipation is

$$\begin{aligned}
\dot{W}_{\text{tot}} &= \dot{W}_{\text{mem}} + \dot{W}_{\text{lub}} \\
&= \int_0^L (RTc(x) - p(x)) Q'(x) dx - \int_0^L Q(x) p'(x) dx \\
&= \int_0^L RTc(x) Q'(x) dx - \int_0^L \frac{d}{dx} (pQ) dx \\
&= \int_0^L RTc(x) Q'(x) dx - [pQ]_0^L \\
&= \int_0^L RTc(x) Q'(x) dx + p(0)Q(0) - p(L)Q(L) \\
&= - \int_0^L RTc'(x) Q(x) dx + (RTc(L) - p(L)) Q(L) - (RTc(0) - p(0)) Q(0)
\end{aligned} \tag{99}$$

In particular, if the concentration is constant, this can be written

$$\dot{W}_{\text{tot}} = (RTc - p(L)) Q(L) - (RTc - p(0)) Q(0). \tag{100}$$

This shows clearly that the driving force in this case is not just the pressure (as in the normal Poiseuille flow), but the “water potential” $p - RTc$. If the velocity is zero at $x = 0$ (as in the analytical solution (41) in Sec. 2) we get the simple form

$$\dot{W}_{\text{tot}} = (RTc - p(L)) Q(L) = 2\pi r_0 L L_p (RTc - p(L))^2 \frac{\tanh m}{m} \tag{101}$$

The individual contributions are similarly

$$\dot{W}_{\text{lub}} = \pi r_0 L L_p (RTc - p(L))^2 \left(-\frac{1}{\cosh^2 m} + \frac{\tanh m}{m} \right), \tag{102}$$

and

$$\dot{W}_{\text{mem}} = \pi r_0 L L_p (RTc - p(L))^2 \left(\frac{1}{\cosh^2 m} + \frac{\tanh m}{m} \right) \tag{103}$$

so when we add these contributions the $\cosh^{-2} m$ terms cancel.

V. SYSTEMS OF PARALLEL PIPES WITH POWER LAW DISTRIBUTION

We now consider a system of parallel, cylindrical pipes as shown in Fig. 5, as it is found in a conifer needle [1, 3, 7]. We follow a stationary flow in one direction x - say, along the central axis of a needle, from $x = 0$ at the tip to $x = L$ at the base. Let $N(x)$ be the number of (cylindrical) tubes at a given x , each of them having a radius $r(x)$. We shall assume that they *interact*, i.e., that the system has a unique velocity $u(x)$ and pressure $p(x)$ shared by the pipes, using the method developed by [3]. The flow rate in each tube is $q(x) = \pi r(x)^2 u(x)$ and the total flow rate is $Q(x) = N(x)q(x)$. In the present work, we shall assume that the pipe-radius is constant, i.e., that $r(x) = r_0$, since this seems to be the case for phloem tubes in conifer needles [7].

The equation for the osmotic water uptake (the “Münch” equation) is then

$$\frac{dQ}{dx} = \pi r_0^2 \frac{dN(x)u(x)}{dx} = 2\pi r_0 N(x) L_p (RTc(x) - p(x)) \tag{104}$$

and Darcy’s law (or Poiseuille’s law)

$$\frac{dp}{dx} = -\frac{8\pi\eta}{\pi r_0^2} u(x). \tag{105}$$

Assuming again that $c(x)$ is a constant, we can divide (104) by $N(x)$ and use (105) to get

$$Q''(x) - \frac{d \log(N(x))}{dx} Q'(x) = 16\eta L_p \frac{1}{r_0^3} Q(x) \tag{106}$$

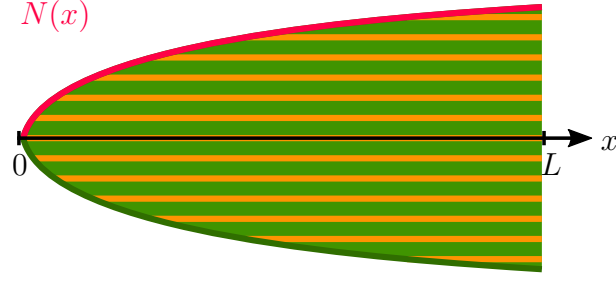


FIG. 5. A system of parallel pipes as in a conifer needle

where the pressure has been eliminated. The constancy of c implies that the loading function is given as

$$\Gamma = \frac{d}{dx} (Q(x)c(x)) = c \frac{dQ}{dx} \quad (107)$$

and will not in general be constant. Using again the dimensionless variable $s = x/L$ we can write this as

$$Q''(s) - \frac{d \log(N(s))}{ds} Q'(s) - MQ(s) = 0 \quad (108)$$

where M is the Münch number (12). If the number of pipes is distributed as a power law

$$N(x) = N_0 \left(\frac{x}{L} \right)^a = N_0 s^a \quad (109)$$

where $N_0 = N(x = L)$ we get

$$Q''(s) - as^{-1}Q'(s) - MQ(s) = 0. \quad (110)$$

To understand the boundary conditions for this equation, we need to go back and look at the pressure through the osmotic intake (104). At $x \rightarrow 0$ this gives

$$\frac{dQ}{dx} = \frac{1}{L} \frac{dQ}{ds} \rightarrow 2\pi r_0 N(s \rightarrow 0) L_p (RTc - p_0) \quad (111)$$

in which we need to determine p_0 , which we assume is going to a constant. This can be done via the Darcy relation (105)

$$p_0 - p(L) = \frac{8\pi\eta}{\pi^2 r_0^4} \int_0^L \frac{Q(x)}{N(x)} dx \quad (112)$$

and if we would e.g. assume that the pipes are open to the outside or a medium with the same pressure as *outside* of the pipes at $x = 0$, we could set $p(L) = 0$ giving

$$p_0 = \frac{8\pi\eta}{\pi^2 r_0^4} \int_0^L \frac{Q(x)}{N(x)} dx. \quad (113)$$

We will, however, keep $p(L)$ as a parameter for the rest of this calculation. The substitution $z = ms$ transforms (110) to the universal equation

$$Q''(z) - az^{-1}Q'(z) - Q(z) = 0 \quad (114)$$

which has a singular point at $z = 0$. The ansatz

$$Q(z) = z^b v(z) \quad (115)$$

leads to the equation

$$z^{b-2} (z^2 v'' + (2b-a)z v' - (z^2 - b(b-1-a))v) = 0. \quad (116)$$

If we set $2b - a = 1$ or $a = 2b - 1$, we get $b(b - 1 - a) = -b^2$ and

$$z^2 v'' + z v' - (z^2 + b^2) v = 0 \quad (117)$$

which is the modified Bessel equation of order b with solutions

$$v(z) = AI_b(z) + BK_b(z) \quad (118)$$

where $I_b(z) \sim z^b$ and $K_b(z) \sim z^{-b}$ for small z . These two solutions correspond to two solutions for Q behaving as x^{2b} and being regular when $x \rightarrow 0$. If we assume that $p_0 \neq RTc$ or at least that p_0 does not diverge at $x = 0$ we conclude that $Q'(x)$ vanishes at $x = 0$ at least like $N(x) \sim x^a$ which means that Q cannot be regular at $x = 0$. On the other hand, the solution going like z^{2b} gives $Q'(z) \sim z^{2b-1} \sim z^a \sim N(z)$ correctly. We finally conclude that $v(z) = AI_b(z)$ or

$$Q(s) = (sm)^b v(sm) = Am^b s^b I_b(ms). \quad (119)$$

From this we get

$$u(s) = \frac{Q(s)}{\pi r_0^2 N(s)} = \frac{A}{\pi r_0^2 N_0} m^b s^{b-a} I_b(ms) = \frac{A}{\pi r_0^2 N_0} m^b s^{1-b} I_b(ms). \quad (120)$$

For small z

$$I_b(z) \approx k_b z^b \quad (121)$$

where

$$k_b = \frac{1}{2^b \Gamma(1+b)}. \quad (122)$$

To fix A we need to integrate u from (120) according to (113)

$$\begin{aligned} p_0 - p(L) &= RTc - p(L) - (RTc - p_0) \\ &= \frac{8\eta}{r_0^2} \int_0^L u(x) dx = \frac{8\eta L}{r_0^2} \int_0^1 u(s) ds = \frac{8\eta LA}{\pi r_0^4 N_0} G_b(m) \end{aligned} \quad (123)$$

where

$$G_b(m) = m^b \int_0^1 s^{1-b} I_b(ms) ds \quad (124)$$

Further, for small s

$$Q(s) = Am^b s^b I_b(ms) \approx Ak_b m^{2b} s^{2b} \quad (125)$$

and

$$LQ'(x) = Q'(s) \approx 2Abk_b m^{2b} s^{2b-1} \approx 2\pi r_0 L N_0 s^a L_p (RTc - p_0) \quad (126)$$

and, again using $2b - 1 = a$ the s -dependence cancels and we get

$$A = \frac{\pi r_0 L N_0 L_p}{bk_b m^{2b}} (RTc - p_0). \quad (127)$$

Using the two equations (123) and (127), we can compute p_0 and A :

$$A = \frac{2\pi r_0 L N_0 L_p}{2bk_b m^{2b} + m^2 G_b(m)} (RTc - p(L)) \quad (128)$$

and for p_0 by

$$RTc - p_0 = \frac{2bk_b m^{2b}}{2bk_b m^{2b} + m^2 G_b(m)} (RTc - p(L)) = \frac{RTc - p(L)}{1 + (2bk_b)^{-1} m^{2(1-b)} G_b(m)}. \quad (129)$$

As $m \rightarrow 0$, $G(m) \sim m^{2b}$ and the RHS approaches 0 and $p_0 \rightarrow 0$ as it should.

To do the integral for $G_b(m)$ we use (see e.g. Gradshteyn and Ryzhik, p. 684)

$$\int_0^1 s^{1-b} I_b(as) ds = a^{-1} I_{b-1}(a) - \frac{a^{b-2}}{2^{b-1} \Gamma(b)} \quad (130)$$

so

$$G_b(m) = m^b \int_0^1 s^{1-b} I_b(ms) ds = m^{b-1} I_{b-1}(m) - \frac{m^{2(b-1)}}{2^{b-1} \Gamma(b)} \quad (131)$$

so that

$$m^2 G_b(m) = m^{b+1} I_{b-1}(m) - m^{2b} k_{b-1} \quad (132)$$

and we are now in a position to evaluate the flux $Q(s)$ from (125):

$$Q(s) = A m^b s^b I_b(ms) \quad (133)$$

$$= \frac{2\pi r_0 L N_0 L_p (RTc - p(L))}{2bk_b m^{2b} + m^2 G_b(m)} m^b s^b I_b(ms). \quad (134)$$

The denominator can be written as

$$2bk_b m^{2b} + m^2 G_b(m) = (2bk_b - k_{b-1}) m^{2b} + m^{b+1} I_{b-1}(m) = m^{b+1} I_{b-1}(m) \quad (135)$$

where the last equality comes from the fact that

$$k_b = \frac{1}{2^b \Gamma(b+1)} = \frac{1}{2^{b-1} 2b \Gamma(b)} = \frac{k_{b-1}}{2b} \quad (136)$$

so $2bk_b - k_{b-1} = 0$. We can then write

$$Q(s) = 2\pi r_0 L N_0 L_p (RTc - p(L)) \frac{s^b I_b(ms)}{m I_{b-1}(m)} = Q_{\max} \frac{s^b I_b(ms)}{I_{b-1}(m)} \quad (137)$$

where

$$Q_{\max} = 2\pi r_0 L_{\text{eff}} N_0 L_p (RTc - p(L)) \quad (138)$$

and the behaviour of $Q(s)$ is shown in Fig. 6, where we have chosen $a = 1/2$ and $b = (a+1)/2 = 3/4$. Note the strong similarity with Fig. 2. In particular the output at $x = L$ is

$$Q(x = L) = Q(s = 1) = Q_{\max} \frac{I_b(m)}{I_{b-1}(m)}. \quad (139)$$

Similarly, we can write the expression for the pressure (129) as

$$\frac{RTc - p_0}{RTc - p(L)} = \frac{2bk_b}{m^{1-b} I_{b-1}(m)}. \quad (140)$$

For small m we find

$$Q(x = L) \rightarrow \frac{1}{2b} 2\pi r_0 L N_0 L_p RTc. \quad (141)$$

For large m we can use the asymptotic behaviour:

$$I_n(x) \approx \frac{e^x}{\sqrt{2\pi x}} \quad (142)$$

together with (139) to get

$$Q(x = L) = Q_{\max} \frac{I_b(m)}{I_{b-1}(m)} \rightarrow Q_{\max} \quad (143)$$

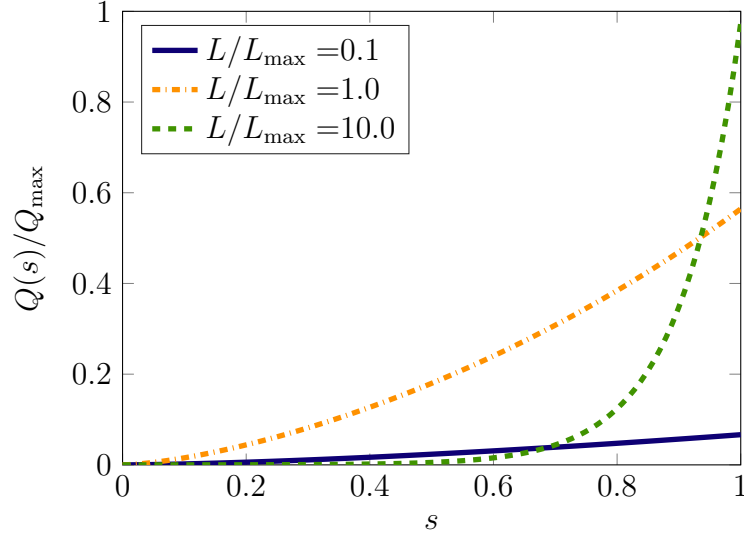


FIG. 6. The function $Q(s)$ given by (137) for $b = 3/4$, scaled by Q_{\max} (138).

which means that the output becomes *independent* of L in this limit (for fixed pressure $p(L)$ at the outlet). Similarly, the pressure p_0 becomes, for large m :

$$\frac{RTc - p_0}{RTc - p(L)} \rightarrow 2bk_b(2\pi)^{1/2}m^b e^{-m} \quad (144)$$

so p_0 approaches RTc exponentially. To compare results at different exponents a (and $b = (a + 1)/2$) we might constrain the system by demanding that the total length of tubes should be fixed. Returning to the density of starting tubes $\rho(x) = N'(x)$, we can express the total “volume” of tubes as

$$\begin{aligned} \frac{V_0}{\pi r_0^2} &= \int_0^L \rho(x)(L - x)dx = \int_0^L N'(x)(L - x)dx = LN(L) - \int_0^L N'(x)x dx \\ &= \int_0^L N(x)dx = L \int_0^1 N(s)ds = \frac{LN_0}{a+1} = \frac{LN_0}{2b} \end{aligned} \quad (145)$$

Using this expression to eliminate $N_0 = 2bV_0/(\pi r_0^2 L)$ in (139) gives the output

$$Q(L) = \frac{4bV_0L_p(RTc - p(L))}{r_0} \frac{I_b(m)}{mI_{b-1}(m)} = 2Q_m \frac{bI_b(m)}{I_{b-1}(m)} \quad (146)$$

where

$$Q_m = \frac{2V_0L_{\text{eff}}L_p}{r_0L} (RTc - p(L)) \quad (147)$$

and we have (again) used (24)

$$m = \frac{L}{L_{\text{eff}}} = 4 \left(\frac{\eta L_p}{r_0} \right)^{1/2} \frac{L}{r_0} \quad (148)$$

The dependence on b with fixed m is shown in Fig. 7. For a single pipe, we have computed the viscous dissipation above and the result is

$$\dot{W}_{\text{tot}} = [(RTc - p) Q]_0^L = (RTc - p(L)) Q(L) \quad (149)$$

since $Q(0) = 0$ and the concentration is constant. In the present model of parallel pipes the dissipation would similarly

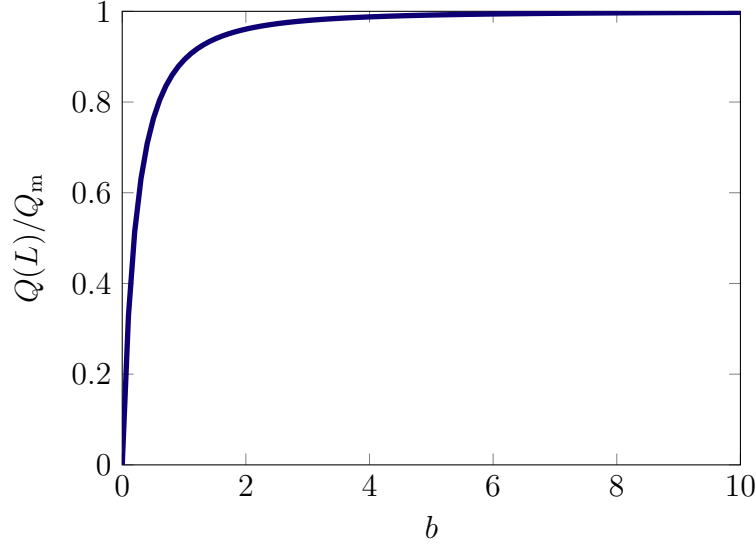


FIG. 7. The function $Q(L, b, m)$ from (146) for $m = 1$, scaled by the value Q_m , given by (147).

be (with $N'(x)$ pipes starting per length)

$$\dot{W}_{\text{tot}} = \int_0^L [(RTc - p) Q]_x^L N'(x) dx \quad (150)$$

$$= (RTc - p(L)) Q(L) \int_0^L N'(x) dx - \int_0^L (RTc - p(x)) Q(x) N'(x) dx \quad (151)$$

$$= N_0 (RTc - p(L)) Q(L) - \int_0^L (RTc - p(x)) Q(x) N'(x) dx \quad (152)$$

$$= \int_0^L N(x) \frac{d}{dx} [(RTc - p(x)) Q(x)] dx. \quad (153)$$

Using

$$Q'(x) = 2\pi r_0 L_p N(x) (RTc - p(x)) \quad (154)$$

we can rewrite \dot{W} as

$$\begin{aligned} \dot{W}_{\text{tot}} &= \frac{1}{2\pi r_0 L_p} \int_0^L N(x) \frac{d}{dx} \left(\frac{Q(x) Q'(x)}{N(x)} \right) dx \\ &= \frac{1}{2\pi r_0 L L_p} \int_0^1 N(s) \frac{d}{ds} \left(\frac{Q(s) Q'(s)}{N(s)} \right) ds \\ &= \frac{1}{4\pi r_0 L L_p} \int_0^1 \left(\frac{d^2}{ds^2} Q^2(s) - \frac{N'(s)}{N(s)} \frac{d}{ds} Q^2(s) \right) ds \\ &= \frac{1}{4\pi r_0 L L_p} \left((Q^2(s))'(1) - (Q^2(s))'(0) - \int_0^1 \frac{d \log N(s)}{ds} \frac{d}{ds} Q^2(s) ds \right) \\ &= \frac{1}{4\pi r_0 L L_p} \left((Q^2(s))'(1) - (Q^2(s))'(0) - a \int_0^1 \frac{1}{s} \frac{d}{ds} Q^2(s) ds \right) \\ &= \frac{1}{4\pi r_0 L L_p} \left((Q^2(s))'(1) - (Q^2(s))'(0) - a \int_0^1 \frac{1}{s^2} Q^2(s) ds - a Q^2(1) \right) \end{aligned} \quad (155)$$

where we have used that $N'(s)/N(s) = a/s$ and that $Q(s) \sim s^b$ for small s , so $Q^2(s)s^{-1} \sim s^{2b-1} = s^a \rightarrow 0$ for $s \rightarrow 0$. Using (137), we have

$$Q(s) = 2\pi r_0 L N_0 L_p RTc \frac{s^b I_b(ms)}{m I_{b-1}(m)} \quad (156)$$

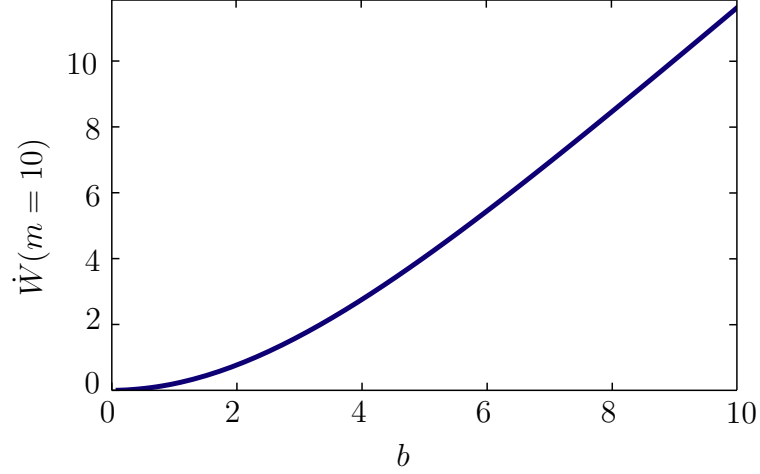


FIG. 8. The function $\dot{W}(b)$ from (155) for $m = 10$.

and, inserting $N_0 = 2bV_0/(\pi r_0^2 L)$

$$Q(s) = \frac{4bV_0L_pRTc}{r_0} \frac{s^b I_b(ms)}{mI_{b-1}(m)}. \quad (157)$$

which should be inserted into (155) to get the final expression. In Fig. 8, we show the dissipation rate for $m = 10$ as function of $b = (a + 1)/2$, and it is monotonically growing with b . This seems to be true for all m .

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